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The gateway to Africa: What determines sea crossing performance of a migratory soaring bird at the Strait of Gibraltar?

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Abstract

1. Large bodies of water represent major obstacles for the migration of soaring birds because thermal updrafts are absent or weak over water. Soaring birds are known to time their water crossings with favourable weather conditions and there are records of birds falling into the water and drowning in large numbers. However, it is still unclear how environmental factors, individual traits and trajectory choices affect their water crossing performance, this being important to understand the fitness consequences of water barriers for this group of birds.
2. We addressed this problem using the black kite *Milvus migrans* as model species at a major migration bottleneck, the Strait of Gibraltar.
3. We recorded high-resolution GPS and triaxial accelerometer data for 73 birds while crossing the Strait of Gibraltar, allowing the determination of sea crossing duration, length, altitude, speed and tortuosity, the flapping behaviour of birds and their failed crossing attempts. These parameters were modelled against wind speed and direction, time of the day, solar irradiance (proxy of thermal uplift), starting altitude and distance to Morocco, and age and sex of birds.
4. We found that sea crossing performance of black kites is driven by their age, the wind conditions, the starting altitude and distance to Morocco. Young birds made longer sea crossings and reached lower altitude above the sea than adults. Crosswinds promoted longer sea crossings, with birds reaching lower altitudes and with higher flapping effort. Birds starting at lower altitudes were more likely to quit or made higher flapping effort to complete the crossing. The location where birds started the sea crossings impacted crossing distance and duration.
5. We present evidence that explains why migrating soaring birds accumulate at sea passages during adverse weather conditions. Strong crosswinds during sea crossings force birds to extended flap-powered flight at low altitude, which may

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increase their chances of falling in the water. We also showed that juvenile birds assume more risks than adults. Finally, the way in which birds start the sea crossing is crucial for their success, particularly the starting altitude, which dictates how far birds can reach with reduced flapping effort.

KEYWORDS

animal tracking, bird migration, crosswind, ecological barriers, powered flight, sea crossing, soaring flight, thermal updrafts

1 | INTRODUCTION

The migration of wild animals has been historically determined by ecological barriers such as oceans, deserts, mountains, rivers, and more recently by human infrastructures and modified landscapes (Alerstam, 1990). These features may influence the path of migration, causing the emergence of migratory divides and detours (Newton, 2008), but often they act as ecological filters, pushing individuals to the limits of their physiological capabilities, and reducing the survival prospects of those less adapted (Gill et al., 2009; Hawkes et al., 2011; Strandberg, Klaassen, Hake, & Alerstam, 2010). In either case, obstacles to migration are known to impact the evolutionary pathways of animal populations (Alerstam, Hedenstrom, & Åkesson, 2003). Despite the vast interest of this topic, there have been obvious methodological difficulties in determining the exact consequences of ecological barriers for migratory animals. This scenario has changed in recent years with the introduction of bio-logging techniques allowing the measurement of relevant behavioural and physiological parameters of individual animals while overcoming ecological barriers (Kays, Crofoot, Jetz, & Wikelski, 2015).

For migrating soaring birds, large water bodies represent major obstacles. Soaring flight relies mostly on thermal updrafts, which are rarely formed over water (Bildstein, 2006). Hence, soaring birds crossing water bodies are forced to engage in flap-powered flight, which is energetically demanding and unsustainable for long distances (Hedenstrom, 1993). For this reason, migrating soaring birds circumvent large water bodies and tend to funnel their routes through isthmuses and short water crossings, often producing spectacular concentrations (Bildstein, 2006).

Sea crossings of soaring birds have mostly been studied by direct observation (e.g. Agostini, Gustin, von Hardenberg, & Panuccio, 2016; Bildstein, Bechard, Farmer, & Newcomb, 2009; Kerlinger, 1985; Miller et al., 2016), but also using radar (Becciu, Panuccio, Catoni, Dell'Omo, & Sapir, 2018; Malmiga, Nilsson, Backman, & Alerstam, 2014; Meyer, Spaar, & Bruderer, 2000, 2003) and GPS tracking (Duriez, Peron, Gremillet, Sforzi, & Monti, 2018; Hake, Kjellen, & Alerstam, 2003; Horton, Bierregaard, Zawar-Reza, Holdaway, & Sagar, 2014; Mellone, Lopez-Lopez, Liminana, & Urios, 2011; Nourani, Yamaguchi, Manda, & Higuchi, 2016; Oppel et al., 2015). It has been shown that different species of soaring birds vary considerably in their abilities to perform sea crossings. Species that alternate between soaring and flapping over land, such as harriers, falcons and small hawks, regularly perform sea

crossings of hundreds of kilometres (Agostini, Panuccio, & Pasquaretta, 2015; Bildstein, 2006; Meyer, Spaar, & Bruderer, 2000) or even thousands in some exceptional cases, such as the Amur falcon *Falco amurensis* and the Eleonora's falcon *Falco eleonora* (Bildstein, 2006; Gschweng, Kalko, Querner, Fiedler, & Berthold, 2008). In contrast, obligate soaring species such as vultures, eagles and large hawks rarely cross more than a few tens of kilometres of sea (Agostini et al., 2015; Bildstein, 2006; Meyer et al., 2000). These species are more prone to congregate in large numbers at narrow sea passages and have been shown to match their sea crossings with favourable weather conditions, such as tailwinds (Bildstein et al., 2009; Kerlinger, 1984; Miller et al., 2016; Panuccio, Barboutis, Chiatante, Evangelidis, & Agostini, 2016). These birds typically move along the coast before attempting to cross the sea and often abort initiated crossings, which illustrates well the difficulty of undertaking sea crossings (Bildstein et al., 2009; Kerlinger, 1985). Exact mortality rates are unknown but there are reports of birds falling into the water and drowning in considerable numbers (Partida, 2007; Zu-Aretz & Leshem, 1983), and this phenomenon has been recently documented in GPS tracking studies (Klaassen et al., 2014; Oppel et al., 2015).

Despite the large amount of studies on this topic, detailed information on how soaring birds behave during sea crossings is still scarce. Observational and radar studies are restricted to the initial phase of the sea crossings and tracking studies are generally based on low GPS resolution data (except Duriez et al., 2018). Here, we used high-resolution GPS tracking and triaxial accelerometry allowing for the estimation of flight behaviour parameters over sea and identifying the characteristics of the sea crossing trajectories. Our model species, the black kite *Milvus migrans*, concentrate in large numbers at narrow sea crossings during their migration between Europe and Africa, such as the Straits of Gibraltar and Bosphorus (Newton, 2008), reflecting its high sensitivity to fly over the sea. This species has also been described as the most sensitive soaring bird to crosswinds at the Strait of Gibraltar, as it was shown to significantly reduce its migratory flow with increasing crosswind speed (Miller et al., 2016). We tracked 73 birds crossing the Strait of Gibraltar at high GPS resolution (0.1–1 Hz) and recorded triaxial acceleration bursts every 3 min, allowing for the description of sea crossing performance parameters, including the quitting of initiated sea crossings, sea crossing duration, distance travelled, track tortuosity, mean ground speed, minimum flight altitude above the sea and flapping behaviour. These parameters were modelled in relation to environmental factors that have been shown to influence the flow of

soaring birds at sea passages, and bird traits and behaviours known to affect soaring flight performance in general (Harel, Horvitz, & Nathan, 2016; Kerlinger, 1984; Miller et al., 2016; Panuccio et al., 2016; Rotics et al., 2016). We hypothesized that sea crossing performance of black kites will be negatively affected by strong crosswinds, low initial flight altitude, distance to Morocco from the crossing starting point, and low solar irradiance (as a proxy of poor thermal uplift); but we expect that it will be positively affected by tailwind and the age of the birds (reflecting earlier experience of sea crossings).

2 | MATERIALS AND METHODS

2.1 | Study site and model species

This study was conducted at the Strait of Gibraltar, which is a narrow sea crossing between Europe and Africa, and the main migration bottleneck for soaring birds travelling along the Western European-West African Flyway (Newton, 2008). During the post-breeding migration of soaring birds, Levanter winds (i.e. easterly wind of 10–20 m/s) are frequent and may last for up to a week at a time (Dorman, Beardsley, & Limeburner, 1995). These winds are known to restrict the passage of soaring birds to Africa (Miller et al., 2016). The black kite is the most common soaring species crossing the Strait of Gibraltar during the post-breeding migration, with 50,000–140,000 individuals counted on an annual basis (Martín, Onrubia, de la Cruz, & Ferrer, 2016). Black kites concentrate at narrow sea passages such as the Straits of Gibraltar and Bosphorus (Newton, 2008), although 2,500–5,000 are known to cross the Mediterranean sea at the Channel of Sicily, a wider

sea passage of 145 km (Pannuccio, Agostini, Mellone, & Bogliani, 2014). Among soaring birds, this species is the most affected by Levanter winds at the Strait of Gibraltar, considerably reducing its migratory flow (Miller et al., 2016). Congregations of several thousand birds can be observed around Tarifa during periods of strong Levanter winds (Miller et al., 2016, and also observed during this study).

2.2 | Tracking data collection

We tracked 73 birds at high GPS resolution while they flew over sea at the Strait of Gibraltar during the post-breeding migration (July–September) of 2012 and 2013. Birds were captured in a walk-in trap ($7 \times 7 \times 3.5 \text{ m}^3$) baited with carrion, located 3.5 km north of Tarifa (36.0426°N , 5.6150°W), during periods of Levanter winds (Figure 1). Each bird was equipped with a GPS-GSM data logger (42 g, TM-202/R9C5 module; Movetech Telemetry, UK, <http://movetech-telemetry.com>) attached as backpacks using a Teflon ribbon harness. Harnesses had a weak-link made of rubber band (in 2012) or biodegradable plastic (in 2013) to allow the loggers to automatically detach in less than a year. Data loggers obtained GPS positions (horizontal and vertical mean error of 1.5 m) every minute over land, and every 10 s from the edge of the Strait of Gibraltar, together with 20-s bursts of 1 Hz triaxial acceleration and GPS every 3 min. Data were uploaded to an internet server via the GPRS network every 2 hr. During captures birds were aged (based on plumage), weighted, the wing chord was measured and their moult score recorded. In addition, a sample of breast feathers was collected for molecular sexing (laboratory protocol followed Han, Kim, Kim, Park, & Na, 2009). The number of juveniles and adults tagged was balanced in each capture.

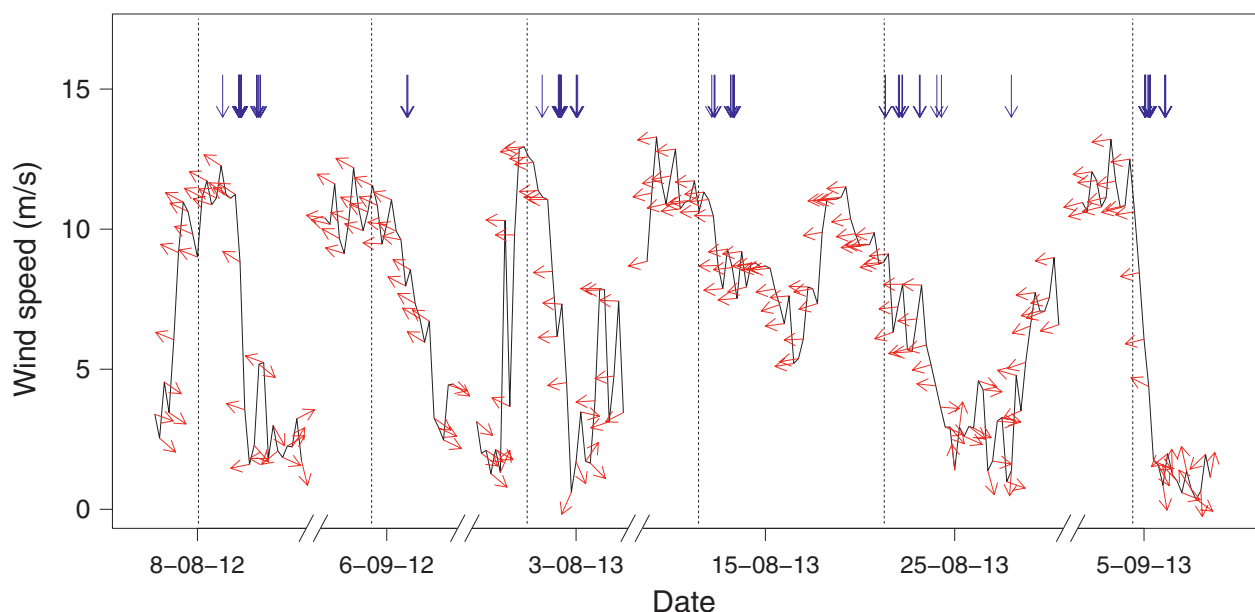


FIGURE 1 Relationship between wind conditions (speed in the y axis and direction as red arrows) and the time when black kites performed the crossing of the Strait of Gibraltar (blue arrows represent crossings of 62 birds). The data is shown for six datalogger deployment events during the post-breeding migrations of 2012 and 2013. Wind data was recorded at weather stations located in Tarifa and Ceuta each 10 min, but it was pooled for each 6 hr to improve readability. Dashed vertical lines correspond to the release of the tagged birds. [Correction added after online publication on 1 May 2020: Figure legends reversed]

The procedures involved in bird trapping and the GPS tagging were approved by the Consejería de Medio Ambiente of the Junta de Andalucía through the license to Alejandro Onrubia.

2.3 | Data analysis

GPS and acceleration data sequences overlapping with the Strait of Gibraltar were selected from the original tracking dataset in order to calculate parameters reflecting the sea crossing performance of the birds. These data included successful sea crossings (62 cases) and flights over sea where birds returned to the Spanish mainland. In the latter cases, some birds did not get far from the coast, which could reflect soaring on the coastal orographic uplift, but those that reached further offshore clearly represented failed crossing attempts, typically showing a V shape path (see Figure 2). Birds that reached more than 500 m offshore (perpendicular to the coastline) and turned back were considered for analysis as to have quitted the sea crossing (40 cases). Therefore, each track included in the analysis was either classified as a successful sea crossing or a failed attempt, providing our first parameter of sea crossing performance. The remaining performance parameters were calculated exclusively for the successful sea crossings. These parameters were:

- Crossing duration (min)—the time difference between the beginning and the end of the sea crossing.
- Distance travelled (km)—the track length.
- Tortuosity—one minus the ratio of horizontal displacement (distance between the track ends) and the distance travelled.
- Mean ground speed (m/s)—the mean of instant speed values obtained for each GPS point.

- Minimum altitude above the sea (m)—the minimum altitude value of the track.
- Mean heave amplitude (g)—the mean of heave amplitudes calculated for each acceleration record in the track. The heave amplitude is the absolute difference between the heave value of an acceleration record in the track and the track heave mean. This variable can be used as a proxy of flapping effort (Halsey, Portugal, Smith, Murn, & Wilson, 2009).

In order to avoid the influence of coastal soaring on these parameters, we excluded the start and end sections of the crossings up to 500 m offshore perpendicular to the coastline.

The parameters of sea crossing performance were modeled with a set of predictors, comprising individual bird traits, weather conditions during the crossing and the starting location and altitude.

These predictors were the following:

- Age—classification into adults ($n = 36$) or juveniles ($n = 37$) based on plumage. The separation between juveniles and adults (second calendar year or older) was unequivocal as juveniles presented fresh plumage while all adults were moulting. Adults were aged with further detail based on the moult patterns (following Forsman, 2016). However, there was low representation across most adult age classes, which justified grouping all non-juvenile birds into a single class in the analysis.
- Sex—classification into male ($n = 36$) or female ($n = 37$).
- Time of the day (h)—the local time when the bird started the over sea flight.
- Starting altitude (m)—the GPS altitude when the bird started the over sea flight.

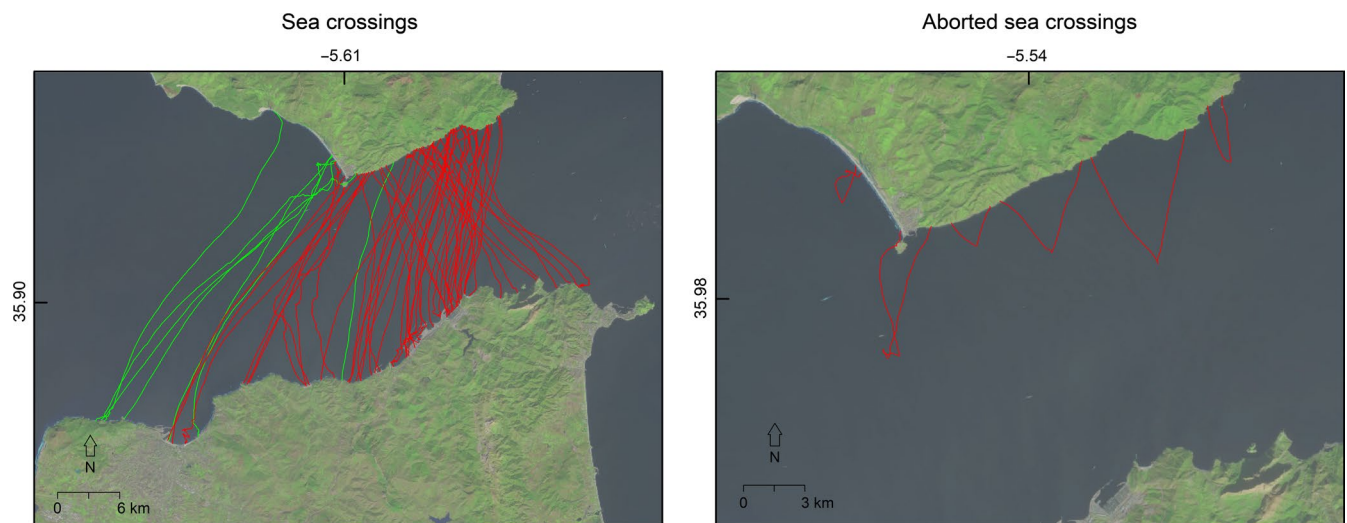


FIGURE 2 Crossings of the Strait of Gibraltar by 62 black kites tracked with high resolution GPS (left) and a sample of failed crossing attempts (right). Green tracks in the left graph were recorded during strong Levanter winds (easterly wind above 10 m/s). The six cases of failed crossings on the right graph were chosen among the 40 recorded in this study in such way that they did not overlap. GPS fixes that based all the tracks shown were acquired each 10 s, with additional 1 Hz bursts of 20 s collected every 3 min. Background is a true-colour Sentinel image acquired on 28 November 2018 (available at the USGS archive, <http://earthexplorer.usgs.gov/>). [Correction added after online publication on 1 May 2020: Figure legends reversed]

- Starting distance to Morocco (km)—the linear distance from the GPS point recorded when the bird started the over sea flight to the nearest point on the Moroccan coastline.
- Tailwind component (m/s)—component of wind velocity vector in the North-South direction. The North-South wind component was calculated from the pooled wind direction and speed values recorded during the sea crossing. Wind data were obtained for every 10 min from a weather station located in Tarifa (36.0138°N, 5.5988°W), except in four periods of a few hours each (on 10, 11 and 12 August 2012 and 6 September 2013) when this weather station malfunctioned and we used wind data from a weather station located in Ceuta (35.8886°N, 5.3469°W). Both weather stations belong to the Spanish state meteorological agency (AEMET).
- Crosswind component (m/s)—component of wind velocity vector either in the east-west direction or the west-east direction. This variable was calculated as described for the tailwind component using the same wind dataset.
- Solar irradiance (min)—solar irradiance at the time when bird started the over sea flight, measured by a sunshine recorder located at Ceuta weather station. This variable can be used as a proxy for thermal uplift (Hernandez-Pliego, Rodriguez, & Bustamante, 2015).

We also recorded bird weight, wing chord and the flight feather area missing due to moult but these variables were excluded from analysis. Bird weight was biased by the amount of food eaten at the trap. Wing length was not possible to measure in many of the adult birds due to the moult of the outer primaries. The use of this variable would create a considerable number of missing values in our modelling dataset. The percentage of flight feather area missing presented too much overlap with the variable age because only the adult birds

were in moult. The use of this variable together with age could cause multicollinearity problems in our models.

We excluded the sea crossing of one bird because it presented extreme values for starting distance to Morocco (25.18 km) and starting altitude (1,569 m), which could influence our models. We also excluded three cases in the models predicting mean heave amplitude due to errors in the accelerometer readings. The variable time of the day was excluded from the models of sea crossings due to high correlation with the variable starting altitude (0.65), but not in the model predicting sea crossing quitting, where the correlation between these two variables was 0.47.

In order to model the probability of birds to quit sea crossings, we fitted a binomial GLMM (through the function `glmer` of the R package `LME4`; Bates, Maechler, Bolker, & Walker, 2016), where the response variable was binomial (crossing or quitting), the predictors were those listed above, and bird identity was included as a random intercept factor. Marginal and conditional R^2 were calculated with the function `r.squaredGLMM` of the `MuMIn` R package (Bartoń, 2019). For all the remaining parameters of sea crossing performance, we fitted linear models (LM, through the function `lm` of the R package `STATS`, R Core Team, 2018) using all the predictors listed above except the variable time of the day. The variable tortuosity was log-transformed to normalize its distribution. Goodness-of-fit was evaluated through R^2 . Fitting assumptions were checked from diagnostic residual plots (through the function `plot.lm` of the R package `STATS`, R Core Team, 2018).

3 | RESULTS

During the tracking of 73 black kites, we recorded 62 successful sea crossings and 40 cases of birds that quitted the sea crossing,

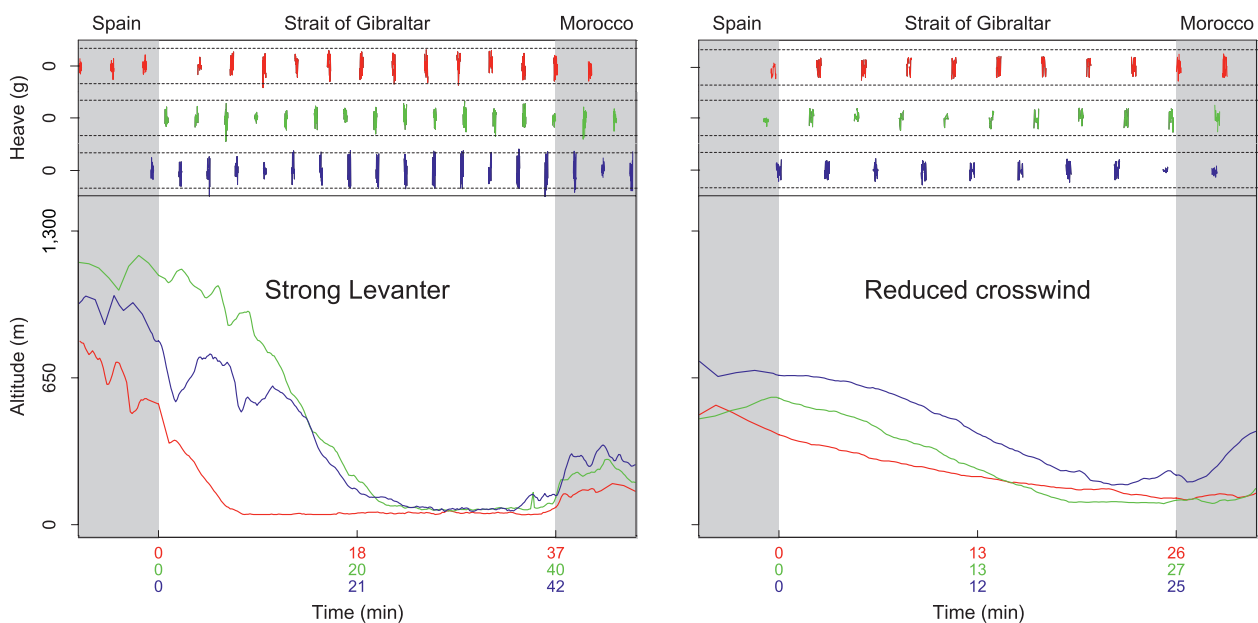


FIGURE 3 Altitude path and acceleration heave of black kites while crossing the Strait of Gibraltar during strong Levanter winds (easterly wind above 10 m/s; left graph) and during periods of reduced crosswinds (wind speed less than 1.5 m/s; right graph). Altitude was recorded each 10 s and acceleration bursts of 20 s were recorded every 3 min. The three birds illustrated in each graph were selected randomly from our dataset. Dashed lines represent the heave amplitude of heavy flapping recorded in four of the tagged birds as they took-off

by turning back to Spanish mainland after having moved more than 500 m offshore (Figure 2). In general, sea crossings tended to happen in the days after the drop of Levanter winds (Figure 1). Birds that challenged strong Levanter winds (over 10 m/s) were visibly dragged westwards, some reaching the coast of Morocco west of Tangier at the edge of the Atlantic Ocean (Figure 2). Typically, birds crossing during Levanter winds left Spain at high altitude but rapidly dropped to altitudes of tens of meters above the sea (Figure 3). These birds engaged in heavy wing flapping (high accelerometer heave), comparable to that of birds taking off (Figure 3). In contrast, birds crossing during weak crosswinds exhibited less flapping amplitude (low accelerometer heave), maintained higher altitude above the sea, and crossed in shorter times (Figure 3).

The probability of quitting sea crossings was only significantly affected by the altitude at the starting point, with birds starting at lower altitudes being more likely to quit and turn back to Spain (Figure 4; Table 1).

The remaining sea crossing performance parameters were significantly affected by bird age, wind conditions and the conditions at the starting point of the sea crossing (Table 2). Juvenile birds took significantly longer time to cross, reached lower altitudes above the sea level and showed lower flapping amplitude than adults (Figure 5; Table 2). The increase of crosswind component was related to longer crossing distance, higher ground speed, higher flapping amplitude and to lower minimum altitude reached during the sea crossing (Figure 6; Table 2). The tailwind component had a negative relationship with the minimum altitude reached by the birds during the crossing (Figure 7; Table 2). The altitude at the starting point of the crossing had a negative relationship with flapping amplitude, and the

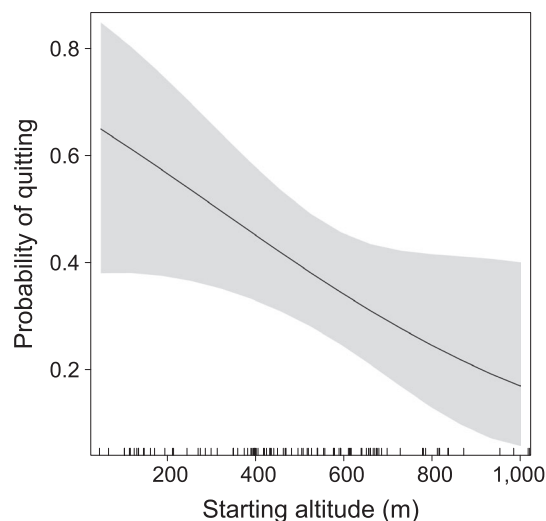


FIGURE 4 Model partial effect of altitude at the starting point of the sea crossing on the probability of quitting. Birds quitting sea crossings inverted their direction in a very obvious way (see Figure 2 for examples). The model is a binomial generalized linear mixed model that includes individual bird traits, weather conditions and the starting location and altitude as predictors of quitting probability, and bird identity as random factor (see Table 1 for details). Shading represents 95% confidence intervals

TABLE 1 Summary statistics of a binomial GLMM relating the probability of quitting sea crossings with individual bird traits, weather conditions and the starting location and altitude. The response variable was assigned to 1 if birds quit the sea crossing or 0 if they successfully reached the coast of Morocco. Bird identity was included as random factor. Marginal and conditional R^2 were calculated with the function `r.squaredGLMM` of the `MuMIn` R package (Bartoń, 2019). SE, standard error; z, Z statistics. The only significant relationship, between quitting probability and starting altitude, is marked in bold and plotted in Figure 4

| | Estimate | SE | z | p | R^2 cond./marg. |
|---------------------|----------|-------|-------|--------------|----------------------|
| Intercept | -6.757 | 4.301 | -1.57 | 0.116 | |
| Age | 0.350 | 0.475 | 0.74 | 0.461 | |
| Sex | 0.587 | 0.493 | 1.19 | 0.234 | |
| Time of the day | 0.199 | 0.130 | 1.52 | 0.127 | |
| Starting altitude | -0.002 | 0.001 | -2.03 | 0.042 | |
| Distance to Morocco | 0.261 | 0.246 | 1.06 | 0.289 | 0.11/0.11 |
| Solar irradiance | 0.063 | 0.054 | 1.18 | 0.239 | |
| Crosswind component | -0.026 | 0.079 | -0.33 | 0.740 | |
| Tailwind component | -0.056 | 0.136 | -0.41 | 0.679 | |

starting distance to Morocco had a positive relationship with the distance travelled to complete the crossing and the crossing duration (Figure 8; Table 2).

Although none of our predictors significantly affected the tortuosity of the sea crossing tracks, juveniles had a nearly significant trend to exhibit more tortuous tracks (Table 2).

4 | DISCUSSION

Although sea crossings of soaring birds have been studied considerably over the last three decades, the use of high-resolution GPS tracking and acceleration allowed us to investigate this phenomenon with unprecedented detail (but see Duriez et al., 2018).

We found that sea crossing performance of black kites at the Strait of Gibraltar was fundamentally driven by their age, the wind conditions over sea, and the starting altitude and distance to Morocco. Matching our hypothesis, juvenile birds showed worse performance than adults by making longer sea crossings and by reaching lower altitude above the sea level (Figure 5). Earlier studies have shown that honey buzzards *Pernis apivorus* tend to undertake longer sea crossings during their first migration (Agostini, 2004; Hake et al., 2003), although the trajectory data of these studies are coarser than ours. Our data clearly show that extended sea crossings challenge birds to prolonged powered flight at very low altitude (Figure 3) that likely increases the chances of fatality due to exhaustion, but we did not record fatalities in our

TABLE 2 Summary statistics of linear models relating sea crossing performance parameters (crossing duration, distance travelled, track tortuosity, mean speed, minimum altitude above the sea and mean heave amplitude) with individual bird traits, weather conditions and the starting location and altitude. In the Tortuosity model the response variable was log-transformed to normalize its distribution. R^2 is presented as indicator of goodness of fit of models. SE , standard error; t , T statistics. Significant relationships are marked in bold and are plotted in Figures 5–8

| | Estimate | SE | t | p | R^2 |
|---------------------|----------|--------|-------|------------------|-------|
| Crossing duration | | | | | |
| Intercept | -18.874 | 14.075 | -1.34 | 0.186 | 0.45 |
| Age | 4.458 | 1.767 | 2.52 | 0.015 | |
| Sex | -0.817 | 1.780 | -0.46 | 0.648 | |
| Starting altitude | -0.005 | 0.003 | -1.60 | 0.117 | |
| Distance to Morocco | 3.080 | 0.962 | 3.20 | 0.002 | |
| Solar irradiance | -2.034 | 2.031 | -1.00 | 0.321 | |
| Crosswind component | 0.342 | 0.304 | 1.13 | 0.266 | |
| Tailwind component | -0.246 | 0.465 | -0.53 | 0.599 | |
| Distance travelled | | | | | |
| Intercept | -7.051 | 10.110 | -0.70 | 0.489 | 0.49 |
| Age | 1.997 | 1.269 | 1.57 | 0.122 | |
| Sex | 0.074 | 1.278 | 0.06 | 0.954 | |
| Starting altitude | -0.001 | 0.002 | -0.54 | 0.589 | |
| Distance to Morocco | 1.474 | 0.691 | 2.13 | 0.038 | |
| Solar irradiance | -1.483 | 1.459 | -1.02 | 0.314 | |
| Crosswind component | 0.873 | 0.218 | 4.00 | <0.001 | |
| Tailwind component | -0.246 | 0.334 | -0.74 | 0.464 | |
| Tortuosity | | | | | |
| Intercept | -1.207 | 2.353 | -0.51 | 0.610 | 0.17 |
| Age | 0.553 | 0.295 | 1.87 | 0.067 | |
| Sex | -0.226 | 0.298 | -0.76 | 0.452 | |
| Starting altitude | 0.001 | 0.001 | 1.46 | 0.151 | |
| Distance to Morocco | 0.081 | 0.161 | 0.51 | 0.616 | |
| Solar irradiance | -0.497 | 0.340 | -1.46 | 0.149 | |
| Crosswind component | 0.051 | 0.051 | 1.01 | 0.317 | |
| Tailwind component | -0.094 | 0.078 | -1.21 | 0.231 | |

(Continues)

TABLE 2 (Continued)

| | Estimate | SE | t | p | R^2 |
|--------------------------------|----------|---------|-------|--------------|-------|
| Mean speed | | | | | |
| Intercept | 12.6881 | 4.8461 | 2.62 | 0.012 | 0.23 |
| Age | -0.4739 | 0.6085 | -0.78 | 0.440 | |
| Sex | 0.3064 | 0.6128 | 0.50 | 0.619 | |
| Starting altitude | 0.0003 | 0.0011 | 0.31 | 0.760 | |
| Distance to Morocco | -0.1780 | 0.3312 | -0.54 | 0.593 | |
| Solar irradiance | -0.5058 | 0.6993 | -0.72 | 0.473 | |
| Crosswind component | 0.3410 | 0.1045 | 3.26 | 0.002 | |
| Tailwind component | -0.0662 | 0.1599 | -0.41 | 0.681 | |
| Minimum altitude above the sea | | | | | |
| Intercept | 173.225 | 117.366 | 1.48 | 0.146 | 0.38 |
| Age | -30.961 | 14.737 | -2.10 | 0.040 | |
| Sex | 6.713 | 14.842 | 0.45 | 0.653 | |
| Starting altitude | 0.017 | 0.027 | 0.61 | 0.548 | |
| Distance to Morocco | -2.182 | 8.021 | -0.27 | 0.787 | |
| Solar irradiance | 9.792 | 16.936 | 0.58 | 0.566 | |
| Crosswind component | -8.039 | 2.532 | -3.18 | 0.002 | |
| Tailwind component | -10.433 | 3.874 | -2.69 | 0.009 | |
| Mean heave amplitude | | | | | |
| Intercept | 0.27480 | 0.10210 | 2.69 | 0.010 | 0.31 |
| Age | -0.02965 | 0.01307 | -2.27 | 0.028 | |
| Sex | -0.00348 | 0.01338 | -0.26 | 0.796 | |
| Starting altitude | -0.00005 | 0.00002 | -1.99 | 0.052 | |
| Distance to Morocco | -0.00350 | 0.00703 | -0.50 | 0.621 | |
| Solar irradiance | 0.01613 | 0.01473 | 1.10 | 0.279 | |
| Crosswind component | 0.00465 | 0.00230 | 2.02 | 0.048 | |
| Tailwind component | -0.00549 | 0.00359 | -1.53 | 0.133 | |

study. Although there is no evidence that juveniles die more than adults while crossing water barriers, recent tracking evidence reported high mortality among juvenile Egyptian vulture *Neophron percnopterus* during the crossing of the Mediterranean sea (Oppel et al., 2015). Interestingly, juvenile black kites showed less flapping effort than adults, judged by a lower mean acceleration heave amplitude (Figure 5). This is likely due to the fact that all adult birds were in active moult, some individuals exhibiting a reduction of the

flight feather area of 10% ($M \pm SD$: 6.1 ± 2.8 ; range: 1.8–10.8) that certainly impacted their aerodynamics. Contrary to our expectations, there were no age differences in the probability of quitting sea crossings. This may indicate that juveniles are more prone to undertake risky crossings given that they lack prior sea crossing experience. We must emphasize, however, that age differences in sea crossing performance may be attenuated by the fact that

black kites undertake sea crossings in mixed aged flocks (authors' observations over several years and also observed in the central Mediterranean route, Panuccio et al., 2014). In this context, the lack of prior experience of juveniles may be compensated by following the movements of adult birds (Chernetsov, Berthold, & Querner, 2004; Maransky & Bildstein, 2001), therefore improving their sea crossing performance.

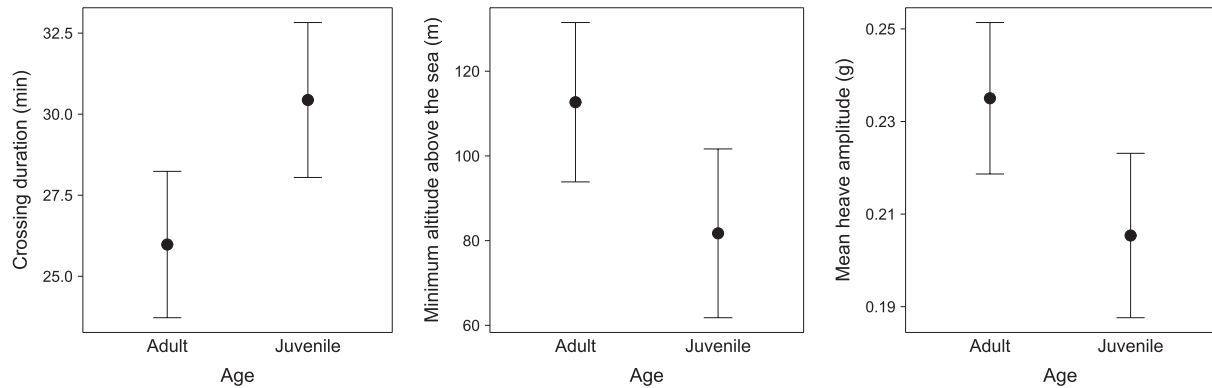


FIGURE 5 Model partial effects of bird age (adult or juvenile) on parameters of sea crossing performance. Crossing duration and minimum altitude above the sea derive from GPS data, and mean heave amplitude is the mean of acceleration heave amplitude values calculated for each individual, which reflects the effort of flapping. Sea crossing performance parameters were extracted from each sea crossing starting from 500 m offshore perpendicular to the coastline of Spain and ending 500 m before reaching the coastline of Morocco in a perpendicular direction. The exclusion of the data close to the coastline prevented the influence of soaring flight at coastal orographic uplift areas. The models are linear models that include individual bird traits, weather conditions and the starting location and altitude as predictors (see Table 2 for details). Error bars represent 95% confidence intervals

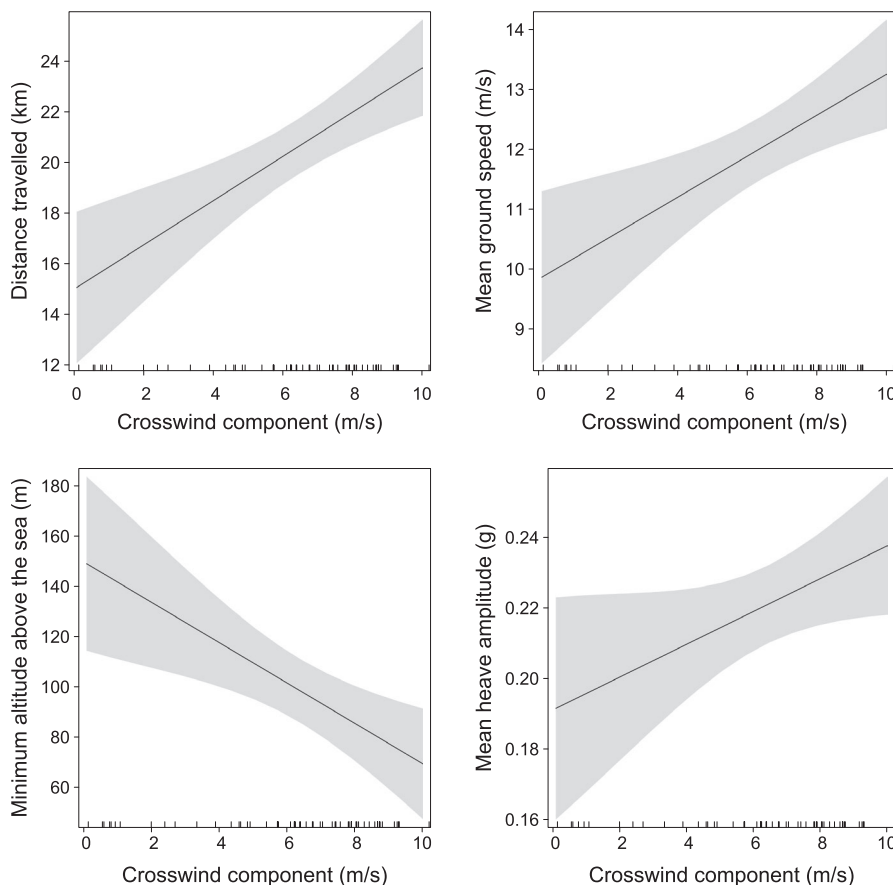


FIGURE 6 Model partial effects of crosswind component on parameters of sea crossing performance. Crossing duration, mean speed and minimum altitude above the sea derive from GPS data, and mean heave amplitude is the mean of acceleration heave amplitude values calculated for each individual, which reflects the effort of flapping. Crosswind component values derive from weather data of 10-min resolution, which were averaged for the period of crossing. Sea crossing performance parameters were extracted from each sea crossing starting from 500 m offshore perpendicular to the coastline of Spain and ending 500 m before reaching the coastline of Morocco in a perpendicular direction. The exclusion of the data close to the coastline prevented the influence of soaring flight at coastal orographic uplift areas. The models are linear models that include individual bird traits, weather conditions and the starting location and altitude as predictors (see Table 2 for details). Shading represents 95% confidence intervals

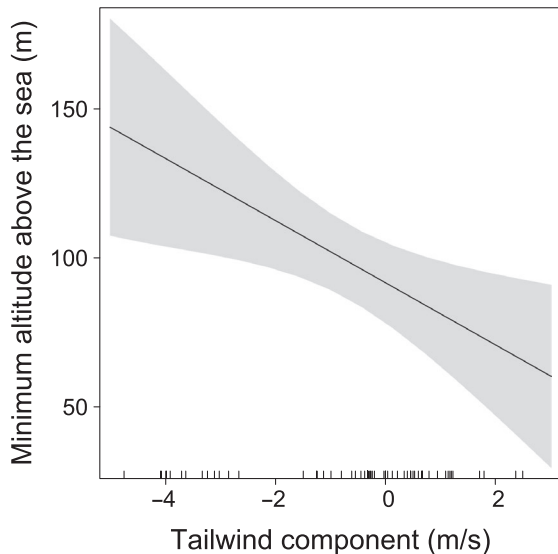


FIGURE 7 Model partial effect of tailwind component on the minimum altitude above the sea reached by the birds during sea crossings. The altitude above the sea derives from GPS data and the tailwind component derives from weather data of 10-min resolution, which were averaged for the period of crossing. Altitude values were extracted from each sea crossing starting from 500 m offshore perpendicular to the coastline of Spain and ending 500 m before reaching the coastline of Morocco in a perpendicular direction. The exclusion of the data close to the coastline prevented the influence of soaring flight at coastal orographic uplift areas. The model is a linear model that includes individual bird traits, weather conditions and the starting location and altitude as predictors (see Table 2 for details). Shading represents 95% confidence intervals

Also matching our hypothesis, sea crossing performance of birds were negatively affected by crosswinds. Higher crosswind component promoted longer sea crossings, with higher flapping effort and

with birds reaching lower altitudes above the sea level (Figure 6). These crossing characteristics illustrate prolonged powered flight, likely with a considerable risk of fatality due to exhaustion. Additionally, the strong easterly crosswinds commonly observed at the Strait of Gibraltar during post breeding migration (Levanter wind) seem to have the potential to drag birds to the open Atlantic Ocean, as suggested by some highly eastward elongated tracks recorded in this study (Figure 2). Not surprisingly, strong crosswinds have been cited as the main reason why birds reduce migration flow over the Strait of Gibraltar, and in other sea passages (Kerlinger, 1984; Meyer et al., 2000; Miller et al., 2016; Nourani et al., 2016). Indeed, our birds were all captured during strong crosswinds and with a few exceptions they waited for crosswinds to drop before undertaking the sea crossing (Figure 1). Crosswind component was positively related with ground speed (Figure 6), suggesting that birds were unable to compensate for the lateral wind to a large extent. A similar pattern was found for soaring birds at the Strait of Messina, with birds increasing ground speeds when drifting with crosswinds blowing towards land (Becciu et al., 2018). However, the opposite pattern was found when crosswinds were blowing towards the sea, suggesting that for such conditions birds strongly compensated the drift (Becciu et al., 2018).

Contrary to our expectations, and the literature (Bildstein et al., 2009; Miller et al., 2016; Nourani et al., 2016; Panuccio et al., 2016), it was not clear from our data that tailwind facilitated sea crossings, although periods of tailwind were relatively rare during the sampling period (Figure 1). Tailwind component was only related to the minimum altitude reached during the sea crossings, with birds reaching lower altitude as the tailwind component was higher (Figure 7). This suggests that when birds were assisted by tailwind, they tolerated flying at lower altitude in a risk-controlled way.

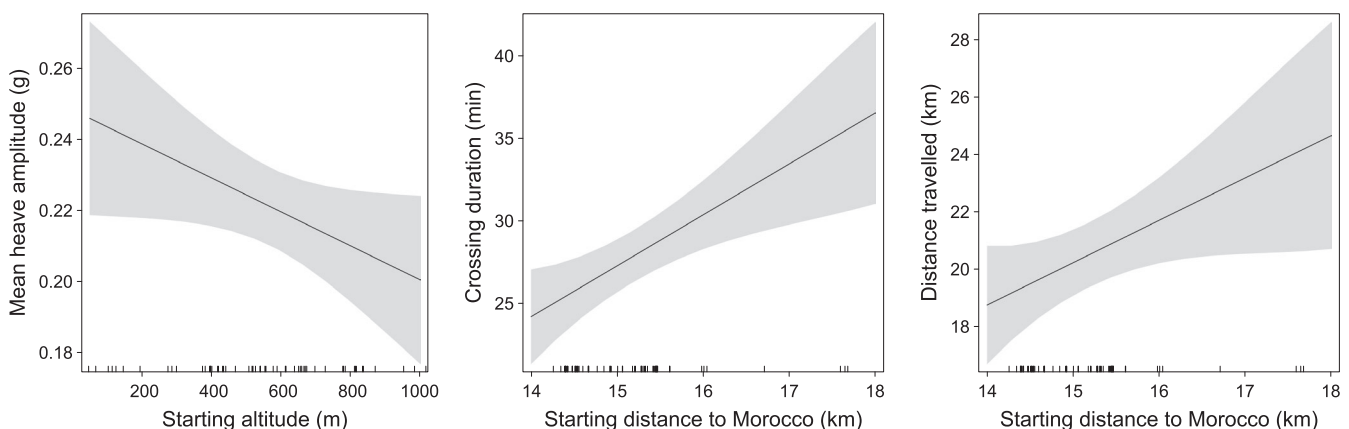


FIGURE 8 Model partial effects of altitude at the starting point of the sea crossing and the linear distance to Morocco on parameters of sea crossing performance. Crossing duration, distance travelled, starting altitude and starting distance to Morocco derive from GPS data, and mean heave amplitude is the mean of acceleration heave amplitude values calculated for each individual, which reflects the effort of flapping. Sea crossing performance parameters were extracted from each sea crossing starting from 500 m offshore perpendicular to the coastline of Spain and ending 500 m before reaching the coastline of Morocco in a perpendicular direction. The exclusion of the data close to the coastline prevented the influence of soaring flight at coastal orographic uplift areas. The models are linear models that include individual bird traits, weather conditions and the starting location and altitude as predictors (see Table 2 for details). Shading represents 95% confidence intervals

The way birds started their sea crossing was also fundamental for their overall performance, as we hypothesized. Birds starting at low altitude significantly increased their flapping effort (Figure 8) and quitted sea crossings more often (Figure 4). Similarly, honey buzzards were shown to avoid starting sea crossings when flying at low altitudes (Panuccio, Gustin, Lucia, Bogliani, & Agostini, 2019). Most sea crossings of black kites started with a long gliding over the sea that was completed with powered flight (Figure 3). It seems obvious that the success of the sea crossing depends largely on how far birds can reach with their initial gliding, which directly depends on how high the gliding starts. It is surprising, however, that there was no influence of solar irradiance, as this variable is directly related with thermal convection (Garratt, 1994), which in turn influences soaring performance of birds (Hernandez-Pliego et al., 2015; Santos et al., 2017). We believe that thermal convection was not a limiting factor for the birds we tracked since most sampling days were bright and the edge of the Strait of Gibraltar is mostly bare soil, which favors the formation of thermal uplift (Santos et al., 2017). In addition, birds starting further away from Morocco obviously extended their crossing duration and distance travelled (Figure 8). Consequently, the distance accomplished with the first gliding was a lower portion of the complete crossing, forcing the birds to prolonged powered flight.

In general, our findings support previous research showing that sea crossings of soaring birds are largely conditioned by local wind conditions (e.g. Kerlinger, 1984; Meyer et al., 2000; Miller et al., 2016; Nourani, Safi, Yamaguchi, & Higuchi, 2018; Panuccio et al., 2016). However, we could further demonstrate that sea crossings during harsh wind conditions demand prolonged powered flight, likely increasing the chances of muscular fatigue that might place birds at risk of drowning or affect the following steps of migration. Although we did not record any fatality, in five cases the birds landed right after the sea crossing or after quitting sea crossings, showing that powered flight is exhausting for this species. We also showed that experience plays a fundamental role in sea crossing performance. Previous research showed that inexperienced birds may not minimize sea crossing distances as they migrate in a broad front (Agostini, 2004; Hake et al., 2003), probably due to orientation limitations (Thorup, Alerstam, Hake, & Kjellen, 2003). However, we show that even when they do find the narrowest sea passages, they do not perform as well as the adult birds. This likely contributes to the higher mortality at sea as it becomes apparent from tracking studies (Oppel et al., 2015). Finally, our results suggest that while there are common among-individual patterns, there is also a level of individuality in the strategies used. Several birds conducted their sea crossings in harsh crosswind conditions placing themselves at high risk, and these were not necessarily inexperienced birds. Other birds started at very low altitudes or at very far distances from Morocco. Whether these decisions were circumstantial or part of a systematic behaviour of individual birds is still an open and very interesting question.

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AUTHORS' CONTRIBUTIONS

C.D.S. and M.W. designed the study; C.D.S., A.-R.M., A.O. and J.P.S. collected the data; C.D.S. and J.P.S. analyzed the data; C.D.S. wrote the manuscript. All authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data available from Movebank Data Repository: <https://doi.org/10.5441/001/1.r9g07dr8> (Santos, Silva, Muñoz, Onrubia, & Wikelski, 2020).

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